NUCELLANGIUM, A NEW GENUS OF FOSSIL SEEDS PREVIOUSLY ASSIGNED TO LEPIDOCARPON

HENRY N. ANDREWS, JR.

Among the more abundant fossils found in the Iowa coal balls are the highly unique "seeds" which have been named *Lepidocarpon glabrum.* These were described by W. C. Darrah in 1941, and in a more recent publication (1949) the same author has continued the discussion with descriptions of included structures which are claimed to be gametophytes and embryos. It is the purpose of this paper to add somewhat to the information given in the published accounts, to point out what appear to the present writer as erroneous statements of fact, and to correct the corresponding conclusions. The fossil is not referable to any known genus, and a new generic name, *Nucellangium,* is proposed herewith for its reception.

Origin of the specimens.—

The specimens on which the present descriptions are based were collected by Mr. Frederick O. Thompson from the Urbandale coal mine located on the western outskirts of Des Moines, Iowa, the exact location having been given in the results of a previous study from this laboratory (Andrews and Kernen, 1946). It should be noted that these specimens and the ones described by Darrah come from the same locality, and through the cooperation of Dr. Elso Barghoorn I have also been able to study a series of similar preparations from the Botanical Museum of Harvard University. There is, therefore, no possibility of confusion in the identity of Darrah's specimens and the ones on which this account is based.

The material is from beds of Middle Pennsylvanian (Des Moines) age; unfortunately the precise stratigraphical equivalence of the Urbandale coal is not known but presumably the material is a little younger than floras known from Illinois No. 6 coal or from above the upper Freeport coal of Pennsylvania.

General introduction to the nature of the fossils.—

We are involved in this discussion with two sets of fossil plants, the first being ovoid bodies presenting certain anatomical characters which lend some justification to their being considered as seeds, and the second less regularly shaped bodies with highly distinctive convolutions extending into their interior which are alleged to represent gametophyte and sporeling.

Certain competent botanists who have examined the fossils in my collection have expressed doubt that the two phases or forms belong to the same species. Mr. Darrah has based his case on the supposition that they represent different growth stages of the same organ. I agree with him to that extent yet it must be remembered that it is not beyond the realm of possibility that we are wrong in this belief.

It seems most convenient to refer to these two forms as *proliferated* and *normal* depending on whether they do or do not contain the supposed sporelings. In view

Issued November 30, 1949.

of the incomplete nature of the previously published accounts it will be necessary to present rather detailed descriptions of the two phases.

I have little doubt that many morphologists will take issue with the usage of terms as they are applied to these fossils. It is becoming clear, however, in groups such as the psilophytes and early coenopterid ferns, that the fossils are not going to make a special effort to comply with our preconceived terminology. It is hoped that the following pages contain descriptions that may be readily comprehended, but I believe that these fossils present structures which do not correspond precisely with known morphological entities.

Insofar as the evidence allows it seems clear that the fossils are sporangia that may or may not have been integumented. It is not known how they were borne on the parent plant and Darrah's restoration of the "strobilus" (1949, fig. 39) is based, so far as I am able to judge, on the supposed general lycopod affinities of the fossil rather than on conclusive evidence. There is a trace of conservatism in the caption to that figure which reads, "Sporophylls not sufficiently known to warrant reconstruction." The fact is that nothing whatsoever is known of the supposed sporophylls.

The general organization of the fossil, with its vascularization and complicated wall structure, seems to allow a closer comparison with a cordaite seed than with a lycopod sporangium. We shall return to such speculations on a later page.

The fossil will be referred to in the following pages as a *sporangium*, as a *nucellus*, or as an (unintegumented) *seed*. The last term is used advisedly and as a matter of convenience, although it seems probable that at least the specimens containing a "seed megaspore" did function as such. It seems most expedient to present first a detailed description of the "normal" fossils and then consider the morphology of the principal structures involved.

The "normal" seeds.—

These are very abundant in the Urbandale coal balls as well as in those from other localities which probably represent the same or a close horizon. In many of the coal-ball specimens examined a half dozen or more are exposed in a single saw cut and, due to the distinctive structure and preservation of the epidermal layer, they are often partially exposed on the broken surfaces of the petrifactions. It is occasionally possible to isolate the seeds intact from the surrounding matrix. While the following description is supplemented by observations on dozens of specimens it is based primarily on a series of transverse sections prepared through a single specimen.

Although there is some variation in the size of the specimens it is not great. They are broadly ovate (figs. 1, 2), averaging 12 mm. long, and in the median region the large and small diameters are 9.5 by 6 mm. Many specimens, particularly the more poorly preserved ones, are crushed and distorted, yet there can be no doubt that the shape and dimensions as given here represent the life form of the seeds.

At one end of these slightly elongated structures, which we will refer to as the proximal end, there is a tiny circular "hilum" scar (fig. 5) representing the point of attachment. At the other end, which will be referred to as the distal end, the seed tapers to a blunt point. Fairly conspicuous ridges lead to this point from the median region of the seed, following the narrow lateral faces. The specimens shown in figs. 1 and 2 present the broad side of the seed and the ridges here form the outline of the photo of the upper half of the seed. The hilum scar may be seen at the proximal end in fig. 1 and the blunt point at the opposite extremity.

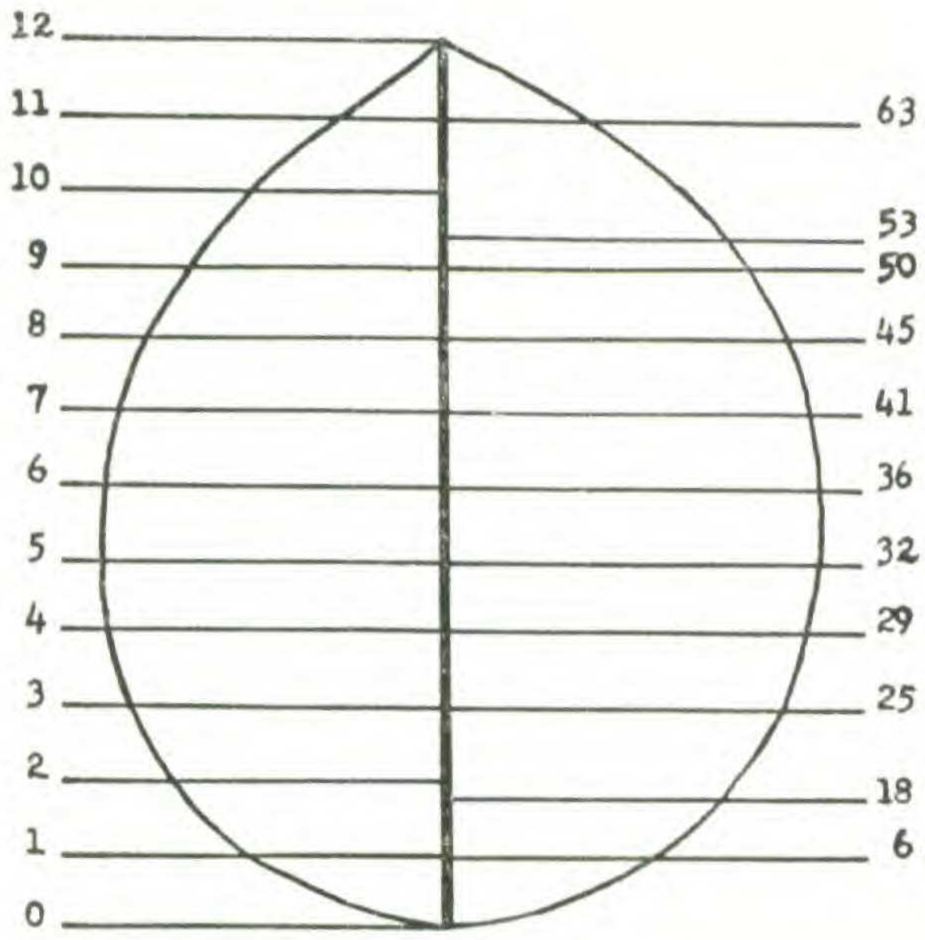
A series of peel preparations has been made by first carefully smoothing a flat surface at the hilum end. Seventy successive peels were then made to within less than a half mm. of the distal end. Particular care was taken to obtain a nearly perfect serial series at the hilum end in order to trace accurately whatever vascular system might be present. When it became evident after working through about one quarter of the length of the specimen that sudden changes in anatomy were no longer taking place the sections were taken further apart in the median region.

It is perhaps apparent that this is a case in which the peel technique is quite indispensable, for it would be only through the greatest good fortune and the use of numerous well-preserved specimens that somewhat comparable results could be obtained by reliance only on ground sections. It is probable that if the specimen had been properly imbedded even better preparations could have been made. However, they were generally removed with little difficulty by using a sharp razor under the low power of a dissecting microscope. Occasionally the epidermis was partially destroyed but since this remains constant in structure from one end to the other there was no loss. Text-fig. 1 indicates the approximate position from which the respective peels were taken.

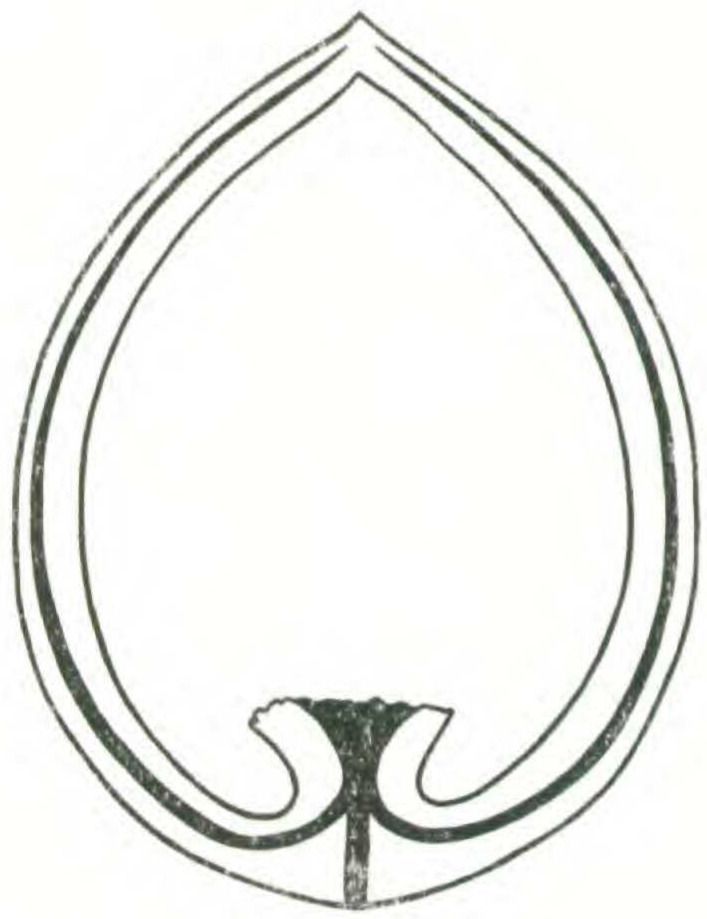
To present an effective description of *Nucellangium* this series of preparations will be followed from proximal to distal end. It may be an aid in following the discussion to note at the outset that three characters set this fossil apart from previously described species of *Lepidocarpon*. These are: a well-developed vascular system with two strands running nearly the entire length of the seed; a thick complex wall including an inner sclerotic layer; and a mode of attachment unlike that of the radially elongated sporangia of other species of *Lepidocarpon*. This combination of characters, and particularly the vascular system, clearly prevents the inclusion of the fossil in that genus.

In the first peel prepared, which does not quite reach the inner limit of the epidermis, the central vascular strand may be distinguished. It is circular in transverse section and is composed of a considerable number of conducting elements (fig. 8). It is apparently purely tracheidal, no parenchyma cells having been observed. The conducting elements of this basal strand, as well as those of the lateral traces, are distinctive in that they are thin-walled, follow a slightly sinuous course, and the bands composing the secondary thickenings are fine and delicate, a condition, judging from the generally good preservation through the specimen, that is natural and not the result of decay. It is not possible to determine

whether the secondary thickenings were of a typical annular or scalariform nature; if the latter, it seems evident that the border of the thickenings was not strongly developed.



Text-fig. 1. Diagrammatic longitudinal view presented as an aid in following the description of the series of transverse peels described on the accompanying pages. Figures at left are millimeters; figures at right represent peel numbers.



Text-fig. 2. Diagrammatic median longitudinal section through the major axis of the seed showing the entrance of the vascular strand at the base and the course of the two branch traces through the length of the wall.

At peel No. 4 a disturbance of the thin-walled parenchyma surrounding the strand suggests a departing trace and when peel No. 6 is reached the tracheids of a branch trace may be observed, not actually leaving the strand but more than half way to the periphery of the seed. At first it was thought that the point of departure had been missed but in the next peel the trace was noted both departing (fig. 6) and in the outer region, as noted above. It is evident, as shown in fig. 10, as well as in text-fig. 2, that the trace dips down slightly after leaving the central strand to follow its course up through the seed. In peel No. 7 the departure of a second trace appears on the opposite side of the central strand.

No other branch traces were observed although a careful search was made, since in his original description Darrah (1941) notes, with reference to the vascular system: "At the proximal end of this seed-like sporangium there is a vascular trace which forks twice, but the four branches quickly exhaust themselves. The bifurcations are at right angles to each other, and by serial sections it has been observed that the two forkings take place one above the other." (p. 97).

The presence of these vascular strands, as I have described them, is of the greatest importance since they are typically absent from lycopod sporangia. It is understandable that they might be readily overlooked in longitudinal sections but

I cannot feel that there is adequate excuse for failing to observe them in the serial sections Darrah indicates were prepared (1941, p. 85).

The pair of traces continues to within less than one half mm. of the distal end of the seed and may be clearly observed in most of the peels throughout the length of the seed; and in the specimen described here there is no suggestion of a second pair of traces. A possible explanation of the *apparent* departure of such will be offered below.

It is clear from all of these transverse peels, with the exception of the basal two or three, that the seeds are bilaterally symmetrical in their anatomy as well as in their gross external form. Taking as an example a nearly median section (fig. 16) the ovate form of the fossil is evident and the two traces may be seen at either end of the great diameter, the traces in this peripheral region occupying a position in extensions of the inner sclerotic layer. Figure 7 shows the trace rather well at a point where it and the surrounding tissues are quite well preserved.

For the purpose of considering the extra-vascular structure of the seed a nearly median point will be taken where a typical sequence of the tissues is displayed. Selecting peel No. 34 (figs. 12, 16) the following may be clearly defined:

The thick-walled, palisade-like epidermis (fig. 9) forms the outer cell layer of the seed over its entire surface with the exception of the hilum scar at the base. These cells are arranged with their long axis approximately parallel to a radius of the seed. They are uniform in size and shape, being about 125 μ long and, when observed in surface view, about 25 μ in diameter. These cells also present an interesting preservation problem. They seem immune to the action of hydrochloric acid, unsuccessful attempts having been made to etch the outer face in order to obtain surface peels. Apparently they are little, if at all, mineralized. It is not surprising that with such an external tissue, so seemingly resistant to an infiltrating mineral solution, the more delicate internal tissues are poorly preserved in most specimens.

Within this epidermal layer is a broad zone of nearly isodiametric, rather thin-walled cells (the outer parenchyma, o. p. of figs. 12, 16). As may be noted in the photos this tissue comprises a major portion of the sporangium wall as a whole. There is a tendency for approximately the outer third of this tissue to have somewhat thicker cell walls than the inner region although there is no sharp distinction into two zones. It is highly significant to the discussion of the morphology of the seed to note that this is clearly *in continuous tissue connection with the conspicuous columnar epidermis.*

Forming a third layer is a very prominent, dark and semi-sclerotic tissue (inner sclerotic layer, i. s. of figs. 12, 16). The term "sclerotic" is perhaps misleading although the cells are somewhat thicker walled than those of the outer parenchyma.

It will be noted (fig. 12) that the cells of this tissue increase appreciably in diameter towards the inner periphery, and they are longitudinally elon-

gated, being at least twenty times as long as they are broad. Where the preservation is good, and nearly perfect longitudinal sections are obtained, the cell walls appear to be strongly pitted. The end walls are transverse or only slightly oblique. The pits (fig. 4) are generally more or less oval-shaped and apparently simple, but whether an actual membrane separated one cell from the next in life cannot be determined. The pitting in some cells is more complex and may even approach reticulate banding. In certain of the more proximal sections in the series of peels taken through the specimen some of the cells of this tissue resemble the tracheidal cells of the traces. It is my suggestion that Darrah may have mistaken these for the second pair of traces mentioned in his account.

The abundant pitting of these cells and their great length as compared with the other non-vascular tissues suggest that their primary function was the conduction of fluids. In studying the seed from base to apex the presence of this tissue is first noted at the level of peel No. 7. From this point to approximately peel No. 11 it develops in abundance in two separate groups, sheathing the departing traces. The two groups soon expand in two C-shaped masses until they unite as a continuous band at the level of peel No. 29. The radial width of this band thereafter gradually increases as is shown in text-fig. 3.

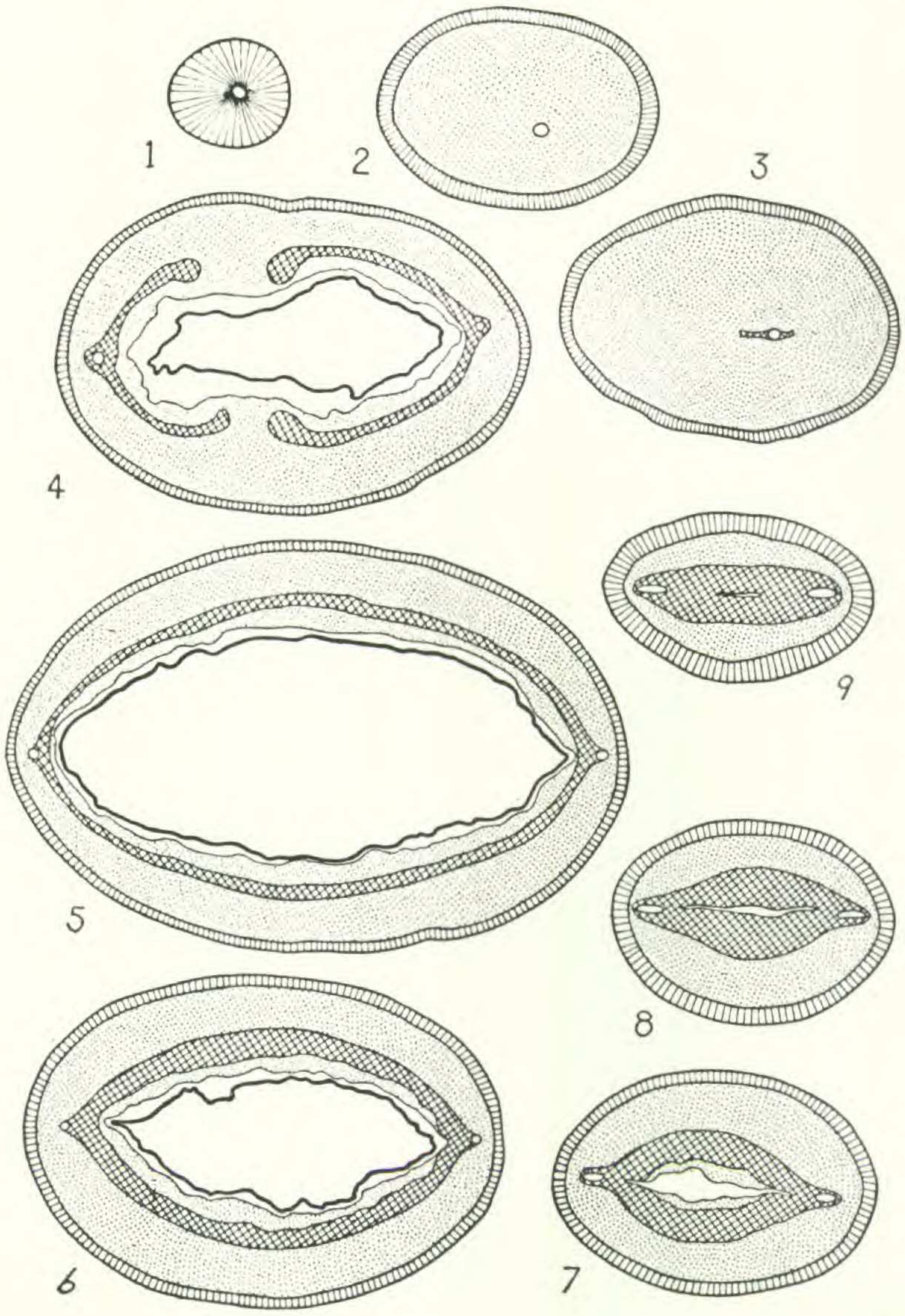
Within the sclerotic layer there is a fourth tissue consisting of very thin-walled cells which in most specimens has been lost through decay. In a few instances, however, it is possible to observe that this tissue did consist of rather thin-walled parenchymatous cells.

Within this fourth tissue layer it is possible, in most sections of the series, to follow a distinct, light yellow band around the periphery of the central cavity. The presence of this structure has been checked in numerous other specimens, and there seems to be no doubt that it is correctly identified as the megaspore membrane. Darrah has succeeded in isolating it very nicely by maceration, a fine illustration being given in his 1949 paper (fig. 11).

No tissue has been observed within this megaspore membrane. The shape of the internal cavity will, however, be described briefly. In following the series of transverse sections from proximal to distal end, at peel No. 10 a small cavity appeared in the position occupied in previous peels by the trace and its accompanying tissue. In peel No. 15 a similar cavity made its appearance on the opposite side and in peel No. 17 the two cavities merged. The fact that one cavity appeared before the other is due to a very slight obliquity in the internal structure of the seed, possibly a slight aberrancy of the particular specimen.

It thus appeared from a study of the serial sections that the internal cavity would be heart-shaped if viewed in median longitudinal section. It has been possible to confirm this supposition from such a nearly median section in the collections of the Harvard Botanical Museum. The basal portion of the specimen is

shown in figure 10. This is a trifle oblique to the median plane so that the actual entrance of the trace into the seed is not shown. The trace does appear, however, as a conspicuous mass of tracheids (fig. 10, t), flaring upwards and terminating the upper part of the cushion or "archesporial pad." A portion of one of the two traces is shown curving down and upward to the left in the outer parenchymatous tissue.



Text-fig. 3. A series of diagrams prepared from representative points in the series of transverse peels described on pages 480–484. 1, peel No. 1; 2, peel No. 3; 3, peel No. 8; 4, peel No. 20; 5, peel No. 38; 6, peel No. 53; 7, peel No. 64; 8, peel No. 66; 9, peel No. 69. Outer lined area, epidermis; stipple, outer parenchyma; cross-hatch, inner sclerotic tissue; inner stipple, inner parenchyma; heavy inner line, megaspore membrane. In 1 only the epidermis and central strand are shown; in 2 the epidermis, outer parenchyma, and central strand; in 3 the epidermis, outer parenchyma, central strand, and beginnings of the inner sclerotic tissue; 4–6 present the complete sequence of tissues with the traces shown at either end of the long transverse axis; 7 is taken above the distal limit of the megaspore.

Before leaving this description of the normal seeds I feel compelled to add a comment on Mr. Darrah's recent paper in which he sums up the distinctive features of these fossils: "Thus far in the development of the sporangium there are no structures or tissues which are unusual. Externally, there is the sporangium wall of usual lepidodendrid construction innermost the megaspore, which can be removed easily by maceration. The tissues between are sterile sporogenous tissues." (1949, p. 3). I do not understand the last sentence but to state that the sporangium wall with its thickness, its complex series of tissues, its vascularization, and its mode of attachment is "of usual lepidodendrid construction" certainly displays a taxonomic freedom that might allow the inclusion of anything within the genus *Lepidocarpon*. Darrah notes further that "My preference for broad rather than narrow interpretations of genera is well known." (p. 12). But surely somewhere there must be limitations.

I feel certain that there is nothing in the literature of lycopod sporangia, living or fossil, which presents a close comparison with this fossil. It is clearly far beyond the bounds of Scott's generic description for *Lepidocarpon* (Scott, 1901) and bears no resemblance to *L. lomaxi*, the type of the genus.

It is perhaps obvious that the principal problem that is involved in correctly interpreting the morphology of this fossil is whether we are dealing with a sporangium or whether it is a true seed. That is, whether the structure described above is a sporangium ("nucellus") enclosing a single fertile megaspore, or whether it is an integument enclosing the remains of a nucellus and the megaspore. I am of course following Darrah's interpretation in accepting the former choice. The reasons for this are as follows: There is no break in the continuity of the four tissues composing the wall of the fossil. They are all clearly in organic connection, there is no delimiting epidermal layer on the inside, and between this innermost parenchymatous layer and the megaspore there is no structure that might be interpreted as the remnants of a nucellus. Furthermore, there is no evidence that a micropylar opening existed at the distal end of the fossil. The tissue appears to be continuous here, allowing access of microspores only by a dehiscence of the sporangium, presumably along the lateral ridges.

Although the outer epidermal layer is very resistant, the shape of the cells and their alignment are as closely comparable to the prismatic epidermis of many cryptogamic sporangia as they are to the epidermis of seed integuments. It has long been recognized that the nucellus, in fact, is a modified sporangium and an epidermal layer so strongly suggestive of its sporangial homology is not surprising in a form that, as far as we know, probably lacks integuments completely.

The "proliferated" seeds.—

Associated with the above-described normal seeds in the Iowa coal balls from the Urbandale mine are other fossils of an even more problematical nature. I believe that they present, as Darrah indicates, a different growth stage than that of the normal specimens. It is freely admitted by the present writer that he is certain of neither their natural affinities nor their morphology but evidence will be

offered to support the contention that the structures described as "gametophytes" and "sporelings" are morphologically one and the same and that they constitute proliferations of sporangial wall tissue.

In the Urbandale coal balls that have passed through my hands some two or three dozens of these proliferated seeds have been observed but, as in the normal ones, a single particularly well-preserved specimen was selected for detailed consideration. However, casual study of the other less well-preserved ones clearly indicates that we are dealing with a typical specimen. In view of the unique nature of the fossils the reader is referred to figs. 18 and 19 as an aid in following the description. These are representative peels taken from specimen No. 519.

The over-all dimensions as illustrated in fig. 19 are 13 × 10 mm. Extending about half way around the specimen (the lower half as it is oriented in figs. 18 and 19) is an epidermis of heavily thickened palisade-like cells which, allowing for some variation among the individuals, agree exactly in size and shape with those of the epidermis of the normal seeds. Within this epidermis there is a parenchymatous tissue which composes the remainder of the fossil. This tissue consists of rather thin-walled cells; it is organically connected with the epidermis; it is vascularized; and it proliferates out into a central area in the form of branches of varying size. Each of these branches contains a delicate vascular strand and is bordered by a well-defined, thin-walled epidermis (fig. 13) which is consequently quite different from the outer epidermis of the fossil as a whole.

It does not seem necessary to comment on the outer thick-walled epidermal layer but a more detailed consideration of the parenchymatous tissue within is very much in order. This consists of rather irregularly shaped cells (fig. 3) in the peripheral region although in the central proliferating arms of tissue (fig. 13) the cells show some tendency to be elongated parallel to the long axis of the arms. It may be noted also in fig. 13 that the epidermis is only slightly differentiated from the interior parenchyma.

It is pertinent to indicate at this point the reasons for correlating these fossils with the previously described normal seeds. The former are, as noted above, somewhat larger and the epidermal layer is split and does not include the entire structure which would be expected if the normal seeds "germinated" to produce the distinctive proliferations shown in figs. 18 and 19. To me, it would seem most likely that the normal seeds or sporangia opened longitudinally along the ridged lateral edges. However, it has not been possible to determine the mechanics of germination from the available specimens, and I find it difficult to glean satisfactory information from Darrah's brief description of this point.

Like the epidermis in the two supposed growth forms, the outer parenchyma of the normal seeds agrees precisely with that of the proliferated seeds. It is clear that the parenchyma is in organic connection with the epidermis just as the epidermis and outer parenchyma of the normal seeds are organically connected, and it is equally clear, as shown in figs. 18 and 19, that there is no break in this parenchymatous tissue from the epidermis to the inner extremity of the arms. The

latter vary considerably in size, some being apparently simple unbranched structures while others branch rather profusely. In the specimen shown in figs. 18 and 19 there may be noted a rather massive central "clump" which gives rise to numerous branches. It will also be noted that many branches appear unconnected with the peripheral tissue but in following the series of peels many of these are readily observed to be connected and I believe that in view of the very close similarity of all of these central islands of tissue (as they appear in an individual peel) there is no reason to doubt that all are so connected. Finally it is important to note that all of these arms are vascularized by a delicate central strand of tracheids similar to those composing the traces of the normal seeds. Although the vascular strands of these are small and composed of few tracheids (fig. 14) the system as a whole is rather extensive. In fig. 18 a tracheidal strand may be noted at *t* and from this lateral strands branch out into the central arms.

Discussion.—

In the opening paragraph of his recent contribution Darrah states that "The discovery of well-preserved fossil embryos in a known plant group is therefore an event of considerable interest." There can be no doubt that such a discovery would be enthusiastically welcomed by botanists in general and paleobotanists in particular, and it is one that may be expected with justification due to the present interest in the coal-ball petrifactions. It is, however, my belief that satisfactory proof of this discovery has not been offered to date. It is not a pleasant task to have to refute the work of a colleague but in view of the seeming importance of these fossils no other course seems feasible. It is very possible that the restorations presented in Darrah's figs. 14–17 and fig. 45 (1949) might well be taken up by writers of text-books and without a first hand knowledge of the fossils it must be admitted that his descriptions are fairly convincing. It is my contention that these restorations showing "Lepidodendroid embryos" within the sporangia are entirely unjustified from the anatomical evidence, that the succession of tissues contained within the fossils has been misinterpreted, and that the evidence does not support the view that they are of lycopod affinities.

I wish to admit freely that satisfactory conclusions regarding the natural relationships of this fossil have not been reached yet. For nearly three years I have pondered over their morphology and affinities and have discussed them with numerous paleobotanists and morphologists. Sincere thanks are due to many of my colleagues for consoling suggestions. These fossils remain as the most problematical ones that I have had occasion to study, but in view of the above-mentioned publications it seemed necessary to present the results of my own observations to date. If future investigations are able to improve on the admittedly vague suggestions offered here they will be received cheerfully.

Darrah (1949) has interpreted the conspicuous peripheral parenchymatous tissue as a gametophyte and certain of the central patches of tissue as portions of

an embryo sporophyte. The basis for his differentiation of sporangial wall (or nucellar) tissue from gametophyte is not apparent in his illustrations or from his description. On page 3 he notes: "Close examination shows that a gametophyte has developed within the megaspore rupturing it and pressing it against the compressed sterile sporangial tissue (remnants of the megaspore membrane can in nearly all cases, be recognized)." And he also notes on this page that "The gametophyte is relatively undifferentiated." And on later pages reference is made to the "more or less disintegrated" gametophyte in more mature specimens in which the embryo sporophyte has developed at the expense of the nucellus and gametophyte.

Thus there is an essential conflict in our descriptions because my sections show clearly that the "gametophyte" and "nucellar" tissues are continuous and the same. Furthermore, no remnants of the megaspore membrane can be defined in any of the proliferated seeds I have examined.

In the well preserved specimen which serves as the basis for the present description there is no evidence of any disorganization of tissue in the peripheral region of the parenchyma adjacent to the epidermis. On the contrary, these two tissues are, as noted above, clearly in organic connection. The general organization and degree of maturity appear to be essentially identical with those described by Darrah. It will be helpful in this respect to compare figs. 18 and 19 with Darrah's figs. 3 and 4.

It would seem, therefore, that there is no justification for referring to a tissue organically connected with the epidermis of a sporangium as gametophyte and sporophyte. I can find no evidence for its alleged development within a megaspore wall. From the prominence of the yellow membrane in the normal seeds there is little question that it would be visible if it were present. It seems especially significant to note that in my specimen the peripheral tissue, that would be termed gametophyte in accordance with Darrah's interpretation, is clearly vascularized. There is no mention of such vascularization in his description, and this oversight may be, in part, responsible for the confusion.

In his fig. 6 Darrah shows what is claimed to be a megaspore membrane in the lower half of his seed and adds that "the tissue outside being in large part, if not entirely, sterile sporogenous tissue." (p. 7). This is a very critical point, and if it is "not entirely, sterile sporogenous tissue" (presumably this means tissue of the sporangium wall) some explanation of what it might be is certainly in order. In view of my own observations there also is doubt regarding the presence of a megaspore membrane in the section Darrah has illustrated. The definition of detail in Darrah's fig. 6 is so inadequate that the reader is afforded no basis for reliable interpretation, and the illustration in no way lends objective support to his conclusions.

Perhaps the most serious criticism that I find necessary to make is one pertaining to the reconstruction (fig. 45) of what is apparently a seed containing a

mature embryo. On page 7 Darrah notes four qualifications relative to this reconstruction. It is stated:

1. That the gametophyte is not shown since it would be more or less disintegrated. Yet no specimen is described in which this stage of development is in any way discernible.

2. That "the sporangium, with an embryo of this degree of development, would be ruptured, probably with the embryonic shoot considerably exserted." But the embryo is shown neatly curled within the unbroken sporangium epidermis.

3. That the "embryo would have a much greater number of leaves, particularly at the growing tip." But the description and illustrations in no way bear this out; and if there were many more leaves present it would seem that this point could have been readily shown in the drawing.

4. That "the orientation of the embryo is variable." I certainly agree that these parenchymatous proliferations are variable but it seems equally evident that they do not represent an embryo.

Following the enumeration of these four qualifications he concludes: "Nevertheless this sketch shows the zones of the embryo in their proper relation, and despite the rather unnatural aspect portrays the characteristics faithfully."

Accurate or even tentative paleobotanical restorations are certainly very much to be desired. Mr. Darrah deserves commendation for taking the trouble to summarize his findings in this form so that those who are not familiar with these fossils may gain a clearer concept of their life form, but to contend that the restoration "portrays the characteristics faithfully" seems to be very much at variance with the observable facts.

We may now return to the normal seeds to consider the supposed correlation of their contained tissues with those of the proliferated seeds. It is probably apparent that the most critical phase of this correlation lies in a determination of the origin of the parenchymatous tissue of the proliferated seeds. If Darrah's contentions are correct one would expect to find some remnants of the sporangial wall (nucellus) tissue, the megaspore membrane, and the gametophyte in those specimens containing immature embryos or even embryos in a rather advanced stage of development. Since no such sequence of disintegrated tissues is in evidence, and since tissues of the supposed gametophyte and sporeling are continuously traceable and connect with the sporangium wall epidermis, some other solution is necessary.

At this point it is pertinent to refer to the inner sclerotic layer of the normal seeds which is shown in figs. 12, 16, and 17. If Darrah's concepts are correct it is hardly possible that this tissue would have been completely disintegrated, yet he makes no mention of it in the germinating seeds. It is not clearly described in his 1941 paper (page 98) but the characteristic sclerenchyma is evident in the top figure of his plate II. No mention is made of the three dimensional aspect and pitting of these cells, so different from any other tissue in either the proliferated or normal seeds. My own observations on the elongate nature and pitting of these

cells were made largely on Darrah's own slides (preserved in the collections of the Harvard Botanical Museum) and it is difficult to understand why it is not given more prominence at least in the specific description, in view of the fact that, like the vascular strands, it is a tissue quite foreign to *Lepidocarpon*.

In his original paper (1941) on *L. glabrum*, following his discussion of the sporangium wall, Darrah notes that within this "The seed megaspore is always present" and in a later sentence adds "The gametophyte is extensive, nearly filling the whole cavity." No further description of the gametophyte is given nor do I find it possible to understand the caption to the lower figure of plate II (1941) in which the gametophyte is said to be present. One might overlook this lack on the assumption that the 1941 paper was a preliminary account but I do not feel that his description of the so-called gametophyte in the 1949 paper can be correlated with its organization as presented in the earlier contribution.

In view of the supplementary factual evidence presented here, the divergent descriptions, based, in part, on the same material, and the conclusion that this fossil cannot be referred to the genus *Lepidocarpon* the following emended diagnosis is given:

Nucellangium glabrum (Darrah) emend. Andrews.

Ovoid seed-like bodies approximately 12 mm. long and 6 × 9.5 mm. in diameter with a small circular hilum scar at proximal end. Presumably a sporangium with a wall consisting of the following sequence of tissues: a thick-walled, columnar epidermis; broad parenchymatous tissue of isodiametric cells; semi-sclerotic, longitudinally elongate, pitted cells; and a narrow thin-walled inner parenchyma. A single large megaspore contained within. Outer parenchyma traversed from base to apex by two delicate vascular strands.

The supposed proliferated form of the fossil somewhat larger, split longitudinally, consisting of the epidermis and outer parenchyma, the latter with numerous proliferating arms that extend approximately into the former area of the central cavity; peripheral region of this parenchyma as well as arms are vascularized.

Locality: Urbandale coal mine, Des Moines, Iowa, and other localities as given by W. C. Darrah, 1941.

Age: Middle Pennsylvanian, Des Moines series.

Specimens on which the present emended description is based are No. 677 and No. 519 in the paleobotanical collections of the Henry Shaw School of Botany.

In the previous accounts no specimens are specifically designated as the type or types. I have, therefore selected the following from Darrah's papers (1941, 1949) for this purpose: As the type for the normal seeds the specimen illustrated in the top figure of plate II (1941), No. 44103 in the collections of the Harvard Botanical Museum. As the type for the proliferated seeds the specimen illustrated in fig. 2 (1949).

Affinities of the fossil.—

I am keenly aware that the following remarks are inadequate as an explanation of the morphology and affinities of this fossil. It is quite evidently an instance in

which it is easier to destroy than to build, and if too much of the former has appeared in the preceding pages at the expense of a constructive treatment it is due partly to a lack of sufficient information and partly to an admittedly inadequate interpretation.

The suggestions that are given below are based, first, on the belief that *Nucellangium* is not a lycopod. At the expense of repetition the reasons for this belief may be briefly reviewed: The complex sporangium wall with its internal "sclerotic" conducting tissue, the vascularization, and the circular hilum scar. These seem to be of fundamental importance and are not in accord with previously described species of *Lepidocarpon*.

Upon the suggestions of at least two competent morphologists, which, incidentally, were offered independently, the possibility has been entertained that *Nucellangium* represents a hydropterid sporocarp. This possibility was supported by the general shape of the fossils, which is not unlike that of a *Marsilea* sporocarp, the mode of attachment, the thick-walled epidermal layer, and the vascularization of the peripheral parenchymatous tissue. However, certain features of the wall of the normal seeds, notably the inner sclerotic tissue and the single large megaspore, are not in accord with such a relationship, and the fertile specimens show no evidence of having borne sporangia after the manner of *Marsilea*. Furthermore, no associated remains are known which present hydropterid affinities. The possibility of such an affinity has, therefore, been abandoned.

Of the pteridophytic groups, other than the lycopods, which are known from the Upper Carboniferous there seem to be none which present a likely comparison. The remaining alternatives are the pteridosperms or cordaites as seed plant groups, or the possibility that we are dealing with an entirely distinct group of fossils, the affinities of which cannot be conjectured. Since the rest of the plant is not known, speculation in the latter direction at present seems useless. For reasons which will be given below it is, therefore, tentatively proposed that *Nucellangium* be considered as a primitive cordaite seed, or, if more noncommittal terminology seems preferable, a cordaite reproductive organ.

In searching for a lead that might suggest relationships with previously described fossils comparisons have been made with some of the many seed compressions. Of these, certain species assigned to the genus *Cardiocarpus* offer at least provocative suggestions. In examining the specimens of *Cardiocarpus* in the Lacoe Collection of the U. S. Geological Survey a few have been noted which correspond very closely to the expected appearance of a compression specimen of *Nucellangium*. For example *Cardiocarpus minor* Newberry (Lacoe coll., U. S. National Museum No. 25421) presents an aspect virtually identical with the profile of the broad face of the *Nucellangium* fossils. A compression of the latter would almost certainly produce a fossil that would be difficult or impossible to distinguish from this species of *Cardiocarpus*.

Although it is somewhat larger, *Cardiocarpus injens* Lesquereux (Lacoe coll., U. S. N. M. No. 25425) may also be mentioned since it displays an epidermal con-

figuration that compares closely with the type of epidermis of *Nucellangium*. *Cardiocarpus bicuspidatus* (Sternberg) Lesquereux, another compression species, also is closely comparable in size and shape with *Nucellangium*.

Since it may have some bearing on the present problem it seems significant to note that the many species assigned to *Cardiocarpus* (approximately 125 species are recorded in the U. S. Geological Survey's Compendium Index of Paleobotany) present an amazing variety of form. Were they better known I believe it is conservative to estimate that a few dozens of natural genera are included in this "compression dumping ground." For want of the necessary anatomical information that might allow a different disposition, these fossils are regarded as "seeds" and at present it seems most plausible that they have their alliance with plants of cordaitean affinities.

In tentatively considering the identity of *Nucellangium* with a species of *Cardiocarpus*, such as *C. minor*, a suggestion of the way in which they may have been borne is presented in Lesquereux's figure of *Cordaianthus spicatus* in the "Coal Flora" (Lesquereux, 1884, III, Pl. 109, fig. 1). Here are seeds of the *Cardiocarpus* type arranged pinnately in two rows on an elongate axis 5 mm. broad. A comparable organization is illustrated by Renault and Zeiller in their 'Flora of Commentry' (Renault and Zeiller, 1888) in figs. 30 and 31 of plate 73. Other authors have figured similar Cordaitalean inflorescences showing seeds of the *Cardiocarpus* type borne apparently terminally on the appendages of short branches. At this point it is perhaps significant to note that the most abundant plant remains in the coal balls from which *Nucellangium* has been obtained are the inflorescences, stems, and leaves of the cordaitales. I am aware that the evidence afforded by association is hardly conclusive, yet in view of the abundance of these cordaitean remains, and the *Nucellangium* fossils which compare closely with compressions known to have been borne on *Cordaianthus* inflorescences, some significance may be attached to this association.

In attempting to postulate a satisfactory explanation of the morphology and affinities of *Nucellangium* it is clear that the unintegumented nature of the fossil is particularly perplexing. I feel quite certain that the normal seeds as described in the earlier portion of this paper represent a nucellus or sporangium wall and in this one respect I seem to be in accord with Mr. Darrah. Is it plausible that we are dealing with an aberrant cordaitean stock whose presence has not been previously suspected? The possibility may exist, of course, as Darrah suggested, that the seeds were shed from their integuments but at present there appears utterly no evidence that would serve even for conjecture.

It is clear that we are dealing with a sporangium possessing a wall that is specialized as a protective device to a very high degree. Certainly the epidermal layer would have served most effectively against the attacks of fungi or small animals and equally well to prevent the loss of water from within. Can it be that we are dealing with a plant in which this protective function of the integument was developed by the sporangium wall, that is, the tissue that would normally have evolved into a nucellus of the more usual type?

With reference to the morphology of the proliferated seeds the problem becomes much more involved. Having discarded the gametophyte-sporeling nature of these bodies some other explanation is clearly in order. It is tentatively suggested that the proliferated specimens could represent either aposporus growths of the outer parenchymatous layer of the nucellus, or a gemma-type reproductive tissue. If any weight can be placed on the suggestion that the proliferations represent an aposporus tissue it would seem likely that archegonia should be found in some abundance, but none have been observed in the specimen described here. It is, moreover, strange that sporelings, as described by Darrah, are so abundant and yet no trace of their earlier stages is present, and only one archegonium has been reported.

The fact that the parenchymatous tissues of the proliferated specimen, both the peripheral region and the internal "arms," are vascularized, is indicative of sporophytic rather than gametophytic tissue. It would seem, therefore, that the most likely function this structure served was as a purely vegetative reproductive organ—that is, a gemma in the broad sense. It is assumed, following this interpretation, that the proliferations developed directly into a new sporophyte plant. Such being the case, it seems likely that the central proliferated "clump" shown in figs. 18 and 19 represents the initial apical meristematic region of the new sporophyte.

The question of course will arise as to the disappearance of the inner sclerotic layer which is so conspicuous in the normal seeds and the only explanation that I am able to offer is that the characteristic development of the proliferated seeds originated before the normal maturation of the internal tissue layers.

Acknowledgment.—

The abundant Urbandale coal balls, containing a wealth of well preserved, unique plants have been gathered by Mr. Frederick O. Thompson of Des Moines. Unfortunately it has not been possible to obtain more of this material in recent years and although we may reasonably hope that other Iowa localities will eventually contribute toward a more satisfactory solution of this and other paleobotanical problems there appears to be little chance of obtaining more Urbandale coal balls. It is partly on this account that the present writer has decided to submit his study of the available specimens of the fossil described above.

It is a pleasure to acknowledge again with gratitude the contributions that Mr. Thompson has made in aid of our investigations of American Carboniferous plants.

Sincere thanks are also due Dr. James M. Schopf for his many helpful suggestions during various stages of this study. The author, however, assumes all responsibility for such criticism, theories, and conclusions as may be found herein.

Bibliography.—

Andrews, H. N. and Jules Kernen (1946). Contributions to our knowledge of American Carboniferous floras. VIII. Another *Medullosa* from Iowa. Ann. Mo. Bot. Gard. **33**:141–147.

Darrah, W. C. (1941). The fossil flora of Iowa coal balls. IV. *Lepidocarpon.* Harv. Univ. Bot. Mus. Leafl **9**:85–100.

————, (1949). Paleobotanical Notices II. Paleozoic Lepidodendroid embryos. Medford, Mass. published by the author.

Lesquereux, L. (1884). Coal flora of the Carboniferous formation. 2nd Geol. Surv. of Penna.

Renault, B. and R. Zeiller (1888). Études sur le terrain houiller de Commentry, Atlas. Soc. del 'Industr. Min., St. Etienne.

Scott, D. H. (1901). On the structure and affinities of fossil plants from the Palaeozoic rocks. IV. The seed-like fructification of *Lepidocarpon*, a genus of lycopodiaceous cones from the Carboniferous formation. Phil. Trans. Roy. Soc. Lond. **194**:291–333.

Explanation of Plate

PLATE 35

Note: A considerable number of the following figures are taken from the series of peels described on pages 481–485. The peel number refers to the respective position as indicated in text-fig. 1. The slide number is the permanent one assigned in the paleobotanical slide collection of the Henry Shaw School of Botany.

Nucellangium glabrum

Figs. 1, 2. Specimens isolated whole from coal balls. The one in fig. 1 displays the hilum scar at the base; this specimen was used in preparing the series of peels described on pages 481–485. × 5.

Fig. 3. Epidermis and outer parenchyma showing the two in organic connection in a proliferated seed. Slide No. 1497. × 85.

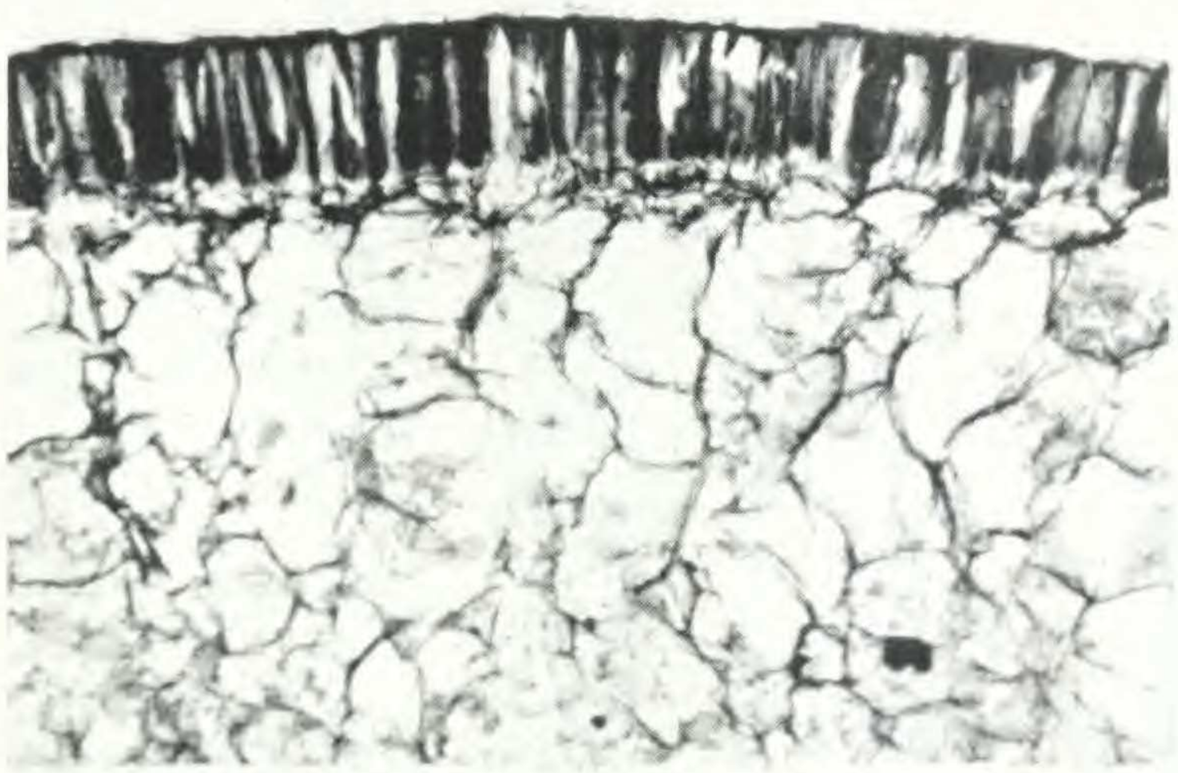
Fig. 4. Cells, showing pitting, of the inner sclerotic tissue of a sterile seed in longitudinal view. From slide No. 50896, collections of the Botanical Museum of Harvard University. × 225.

Fig. 5. Hilum scar of the specimen shown in fig. 1. × 20.

Fig. 6. Photograph of peel No. 9 (slide No. 1643) showing central vascular strand (near base of seed) in right center, and departing trace at left. × 110.

1

2

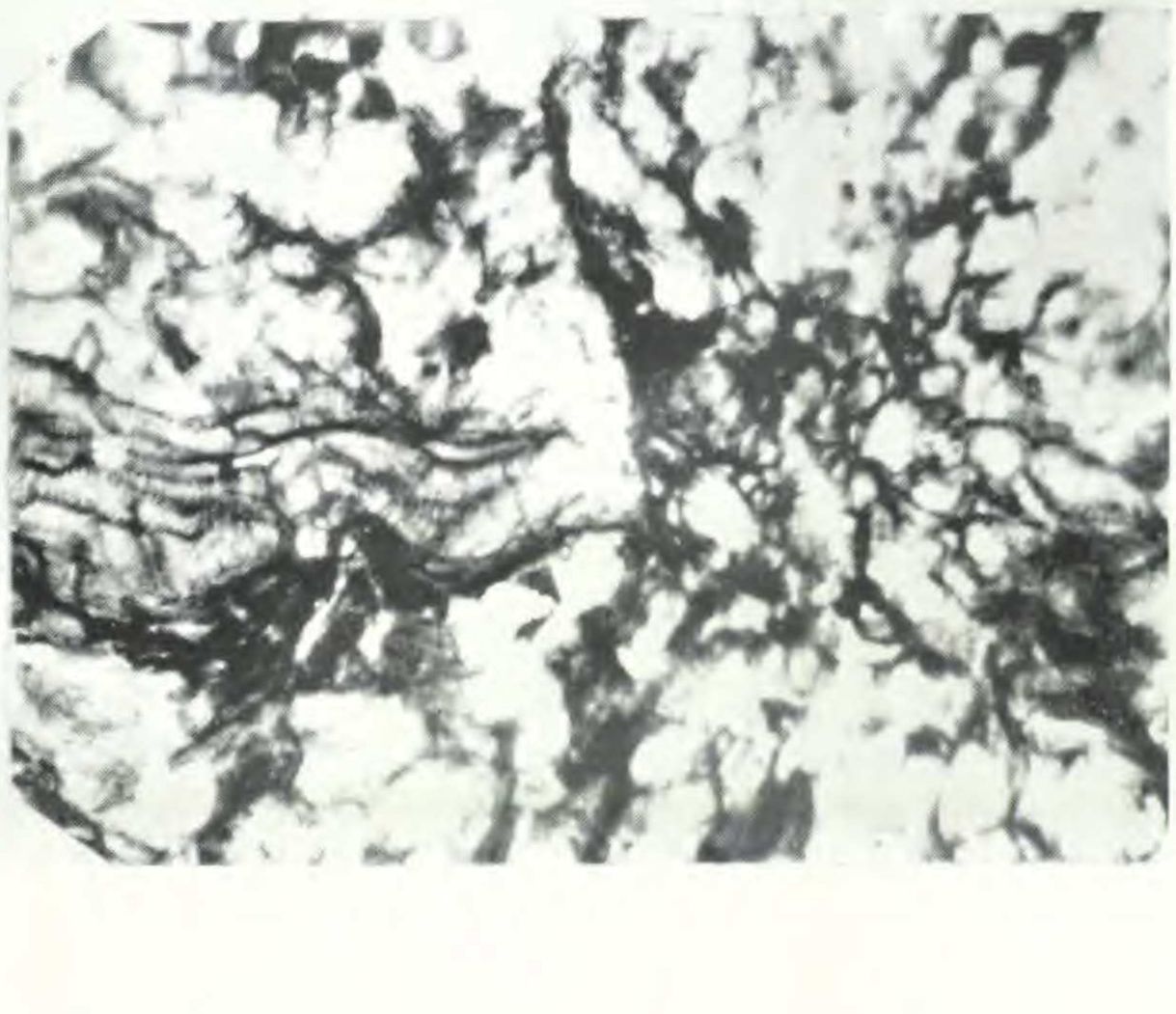


3

4

5

6



Explanation of Plate

PLATE 36

Nucellangium glabrum

Fig. 7. Part of transverse section through the median region of a seed showing the vascular trace on that side. From slide No. 50897, collections of the Botanical Museum of Harvard University. × 54.

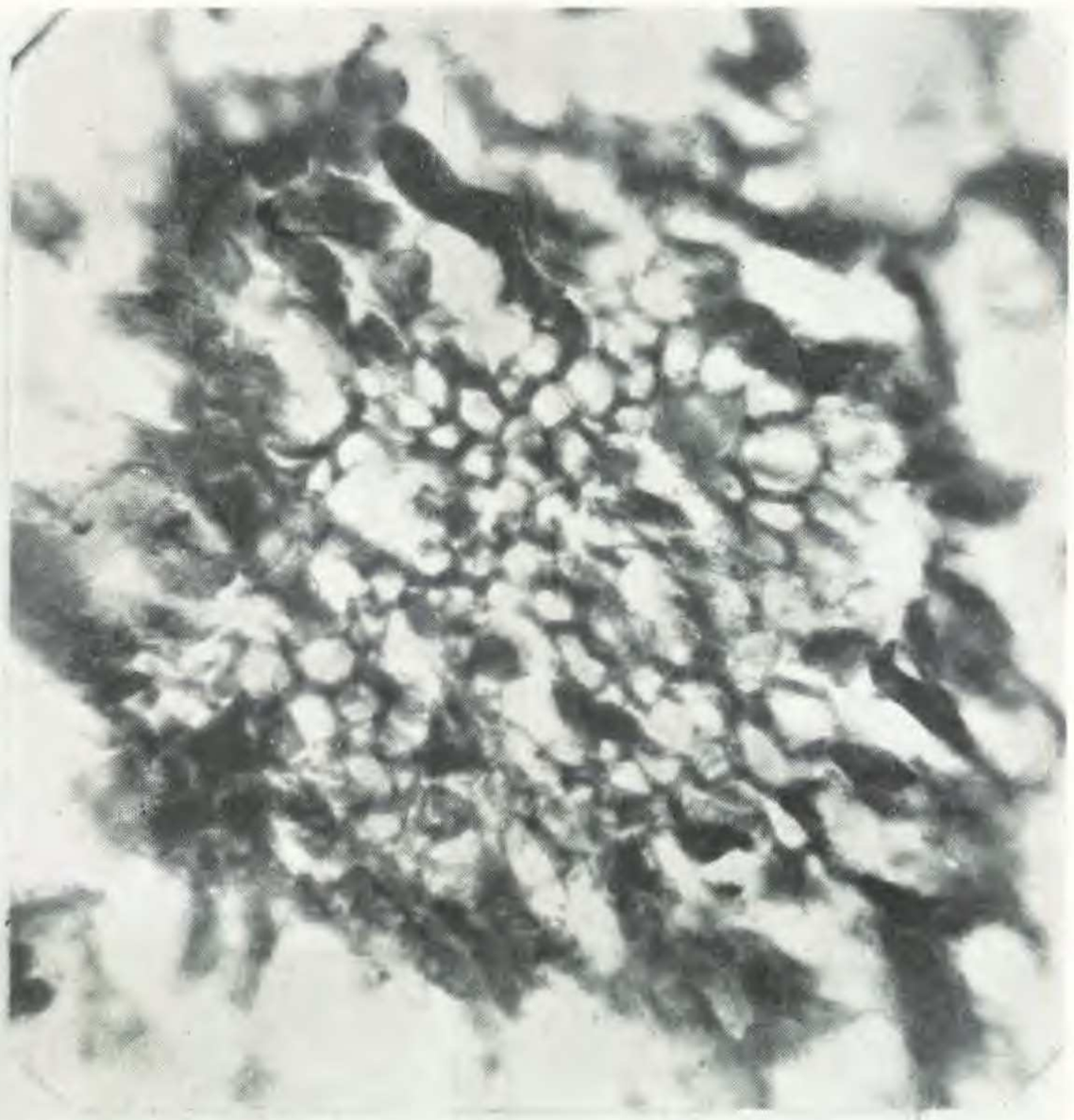
Fig. 8. The central vascular strand in the base of the seed, from peel No. 13 (slide No. 1647). × 220.

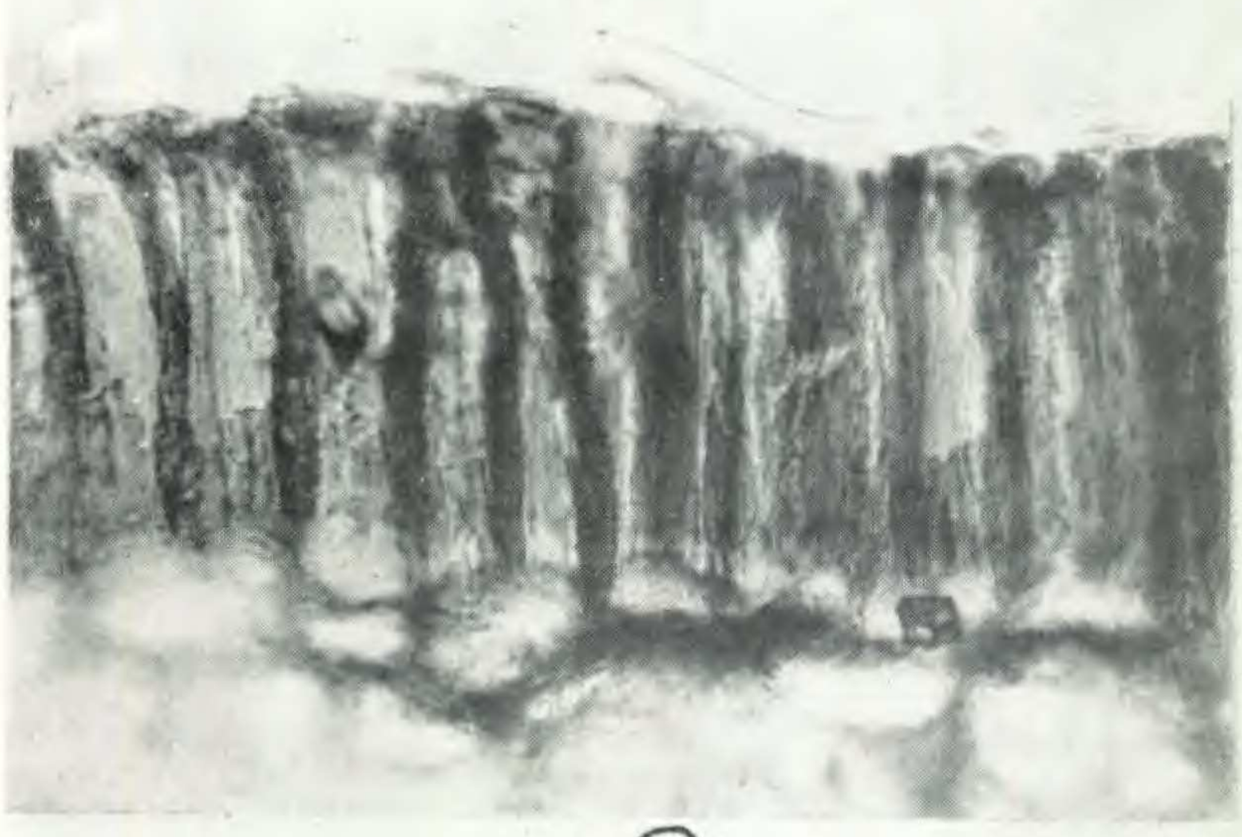
Fig. 9. Section through epidermis of normal seed, from peel No. 34 (slide No. 1656). × 280.

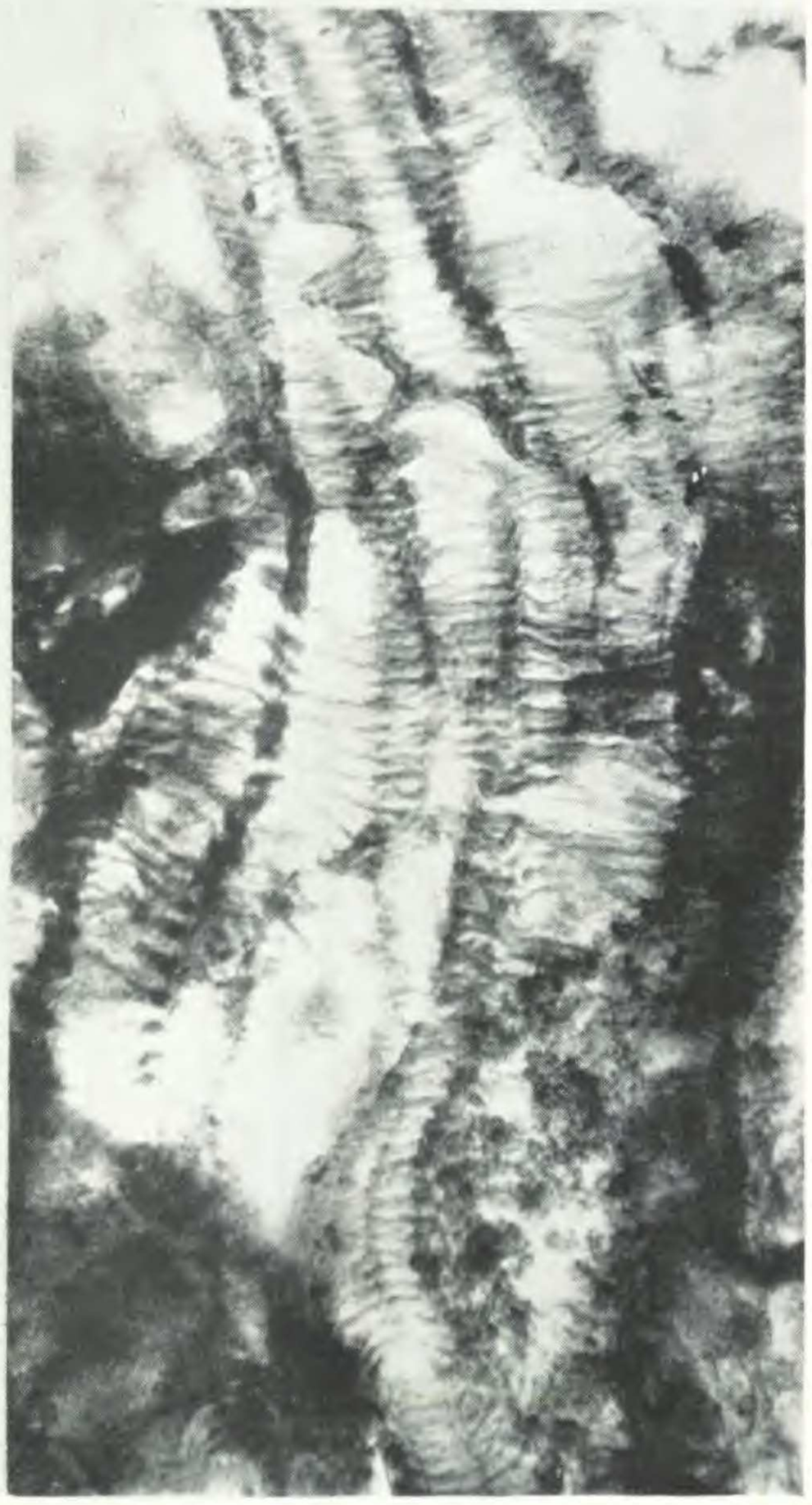
Fig. 10. A nearly median longitudinal section through the basal portion of a seed. *t*, tracheidal tissue in "archesporial pad." From slide No. 50895, collections of the Botanical Museum of Harvard University. × 16.

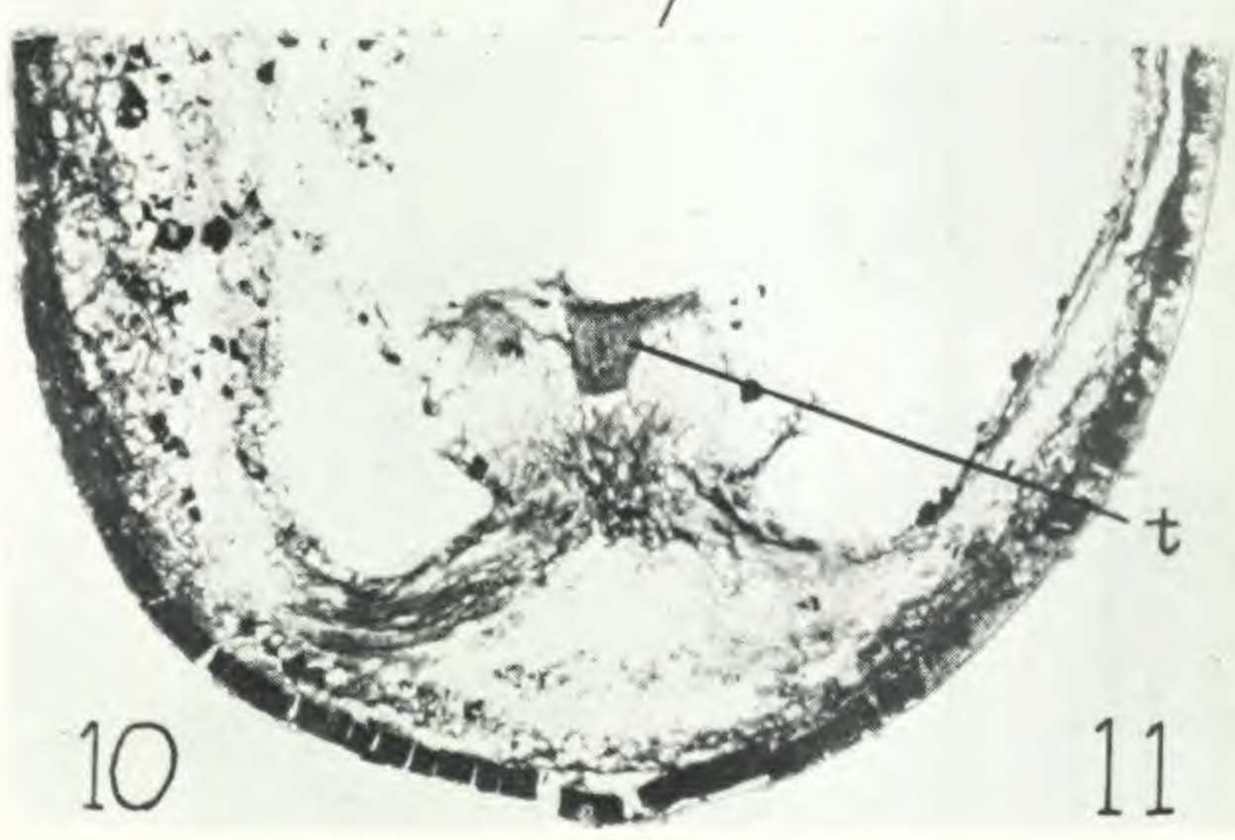
Fig. 11. A highly magnified view of a branch trace of the normal seed, from peel No. 8 (slide No. 1642). × 500.


7
t


8


9


11


10
t

Explanation of Plate

PLATE 37

Nucellangium glabrum

Fig. 12. Transverse section through the wall of the normal seed, from peel No. 34 (slide No. 1656): *e*, epidermis; *op*, outer parenchyma; *is*, inner sclerotic layer; *ip*, inner parenchyma; *m*, megaspore membrane. × 65.

Fig. 13. One of the central arms, or branch proliferations, from the specimen in fig. 18. Slide No. 1496. × 80.

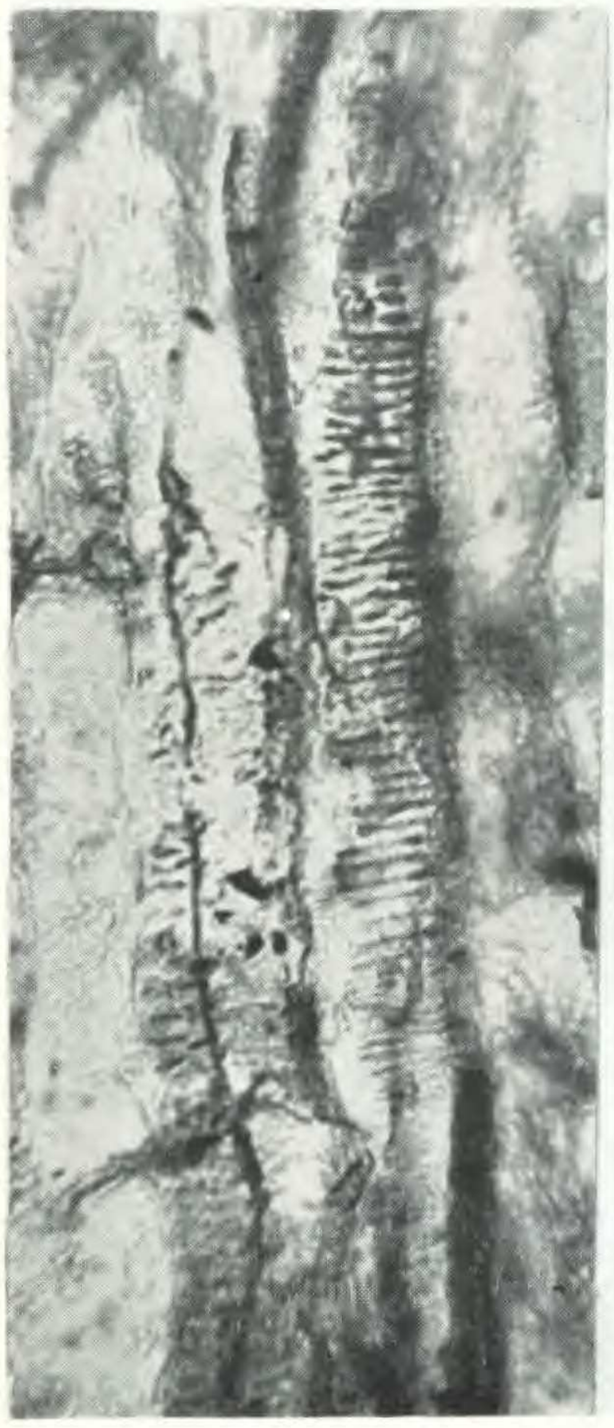
Fig. 14. A vascular strand of the proliferated specimen (fig. 18). Slide No. 1498. × 440.

Fig. 15. A section in the transverse plane through a normal seed taken at one side of the central basal strand. The dark tissue represents the lowermost extension of the inner sclerotic tissue. This is associated at this level with the departing traces and is shown in text-fig. 3 (3) as the small central cross-hatched areas. From peel No. 11 (slide No. 1645). × 80.

12

13

14



15

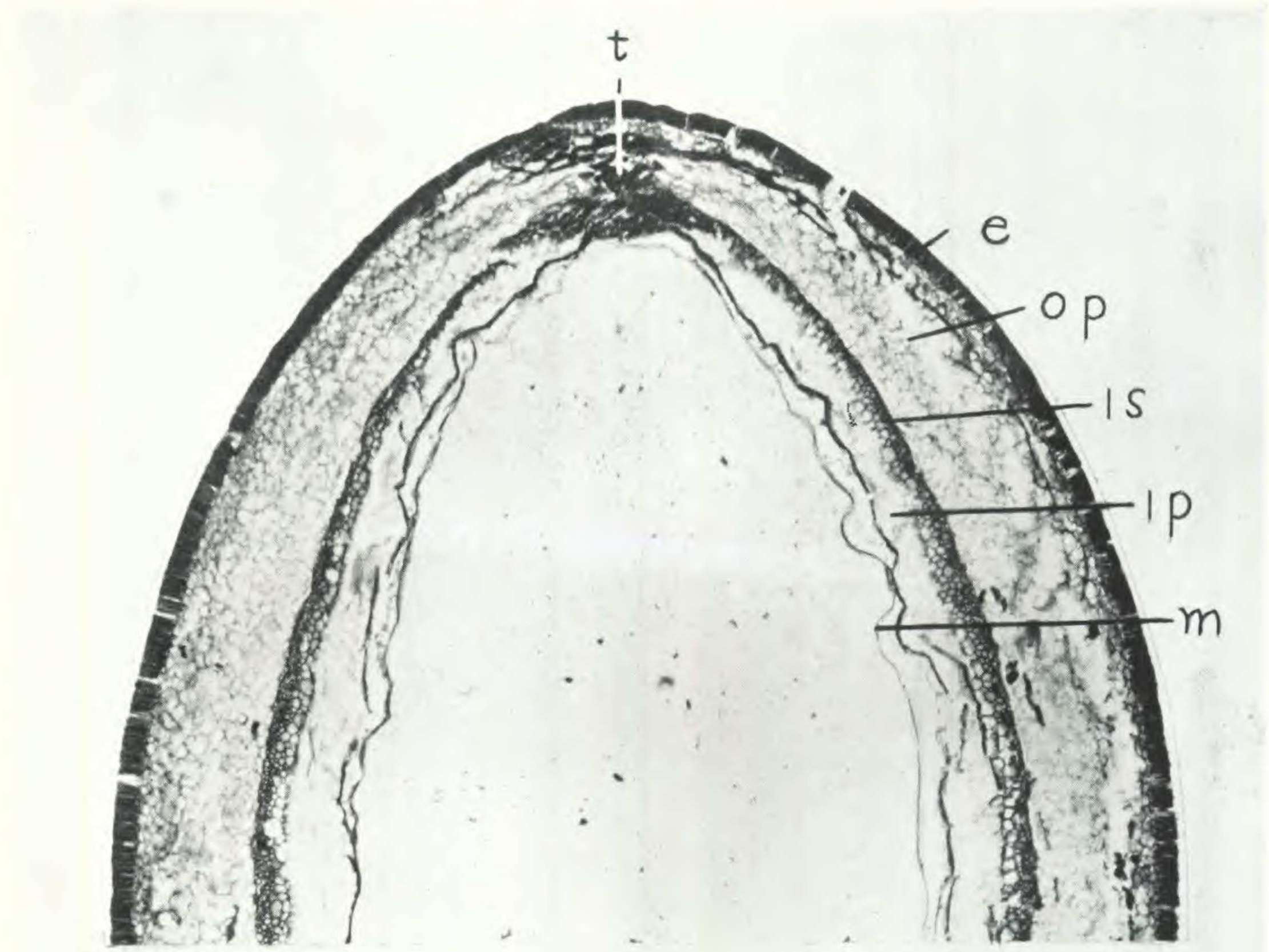
Explanation of Plate

PLATE 38

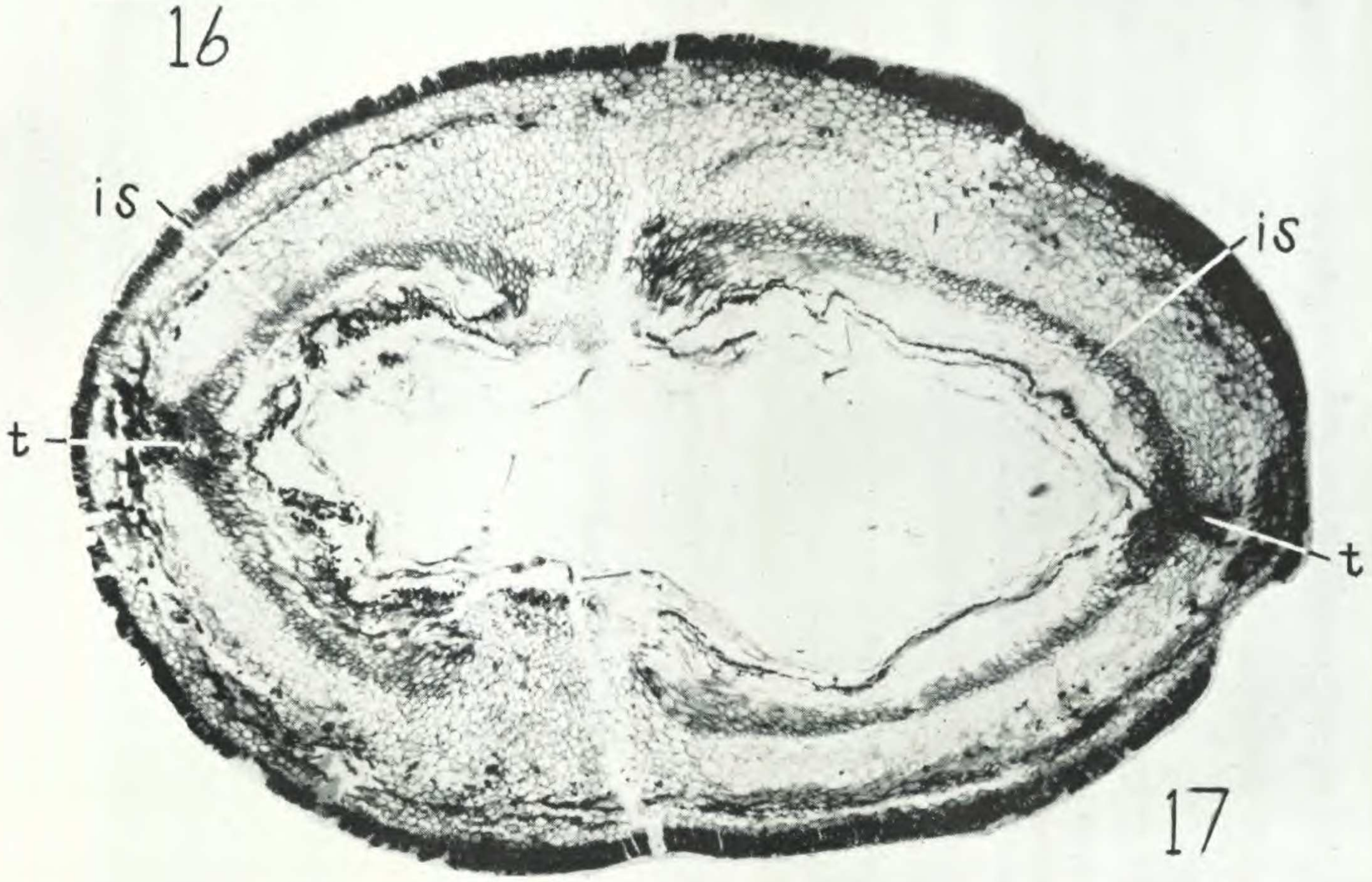
Nucellangium glabrum

Fig. 16. Photograph showing half of the transverse section of the normal seed, peel No. 38 (slide No. 1658): *e*, epidermis; *op*, outer parenchyma; *is*, inner sclerotic layer; *ip*, inner parenchyma; *m*, megaspore membrane; *t*, vascular trace. × 20.

Fig. 17. Complete transverse section of the normal seed, peel No. 20 (slide No. 1653): *t*, position of traces; *is*, inner sclerotic layer. Note interruptions of the inner sclerotic layer on the two sides; compare with text-fig. 3 (4). × 18.



16



17

EXPLANATION OF PLATE

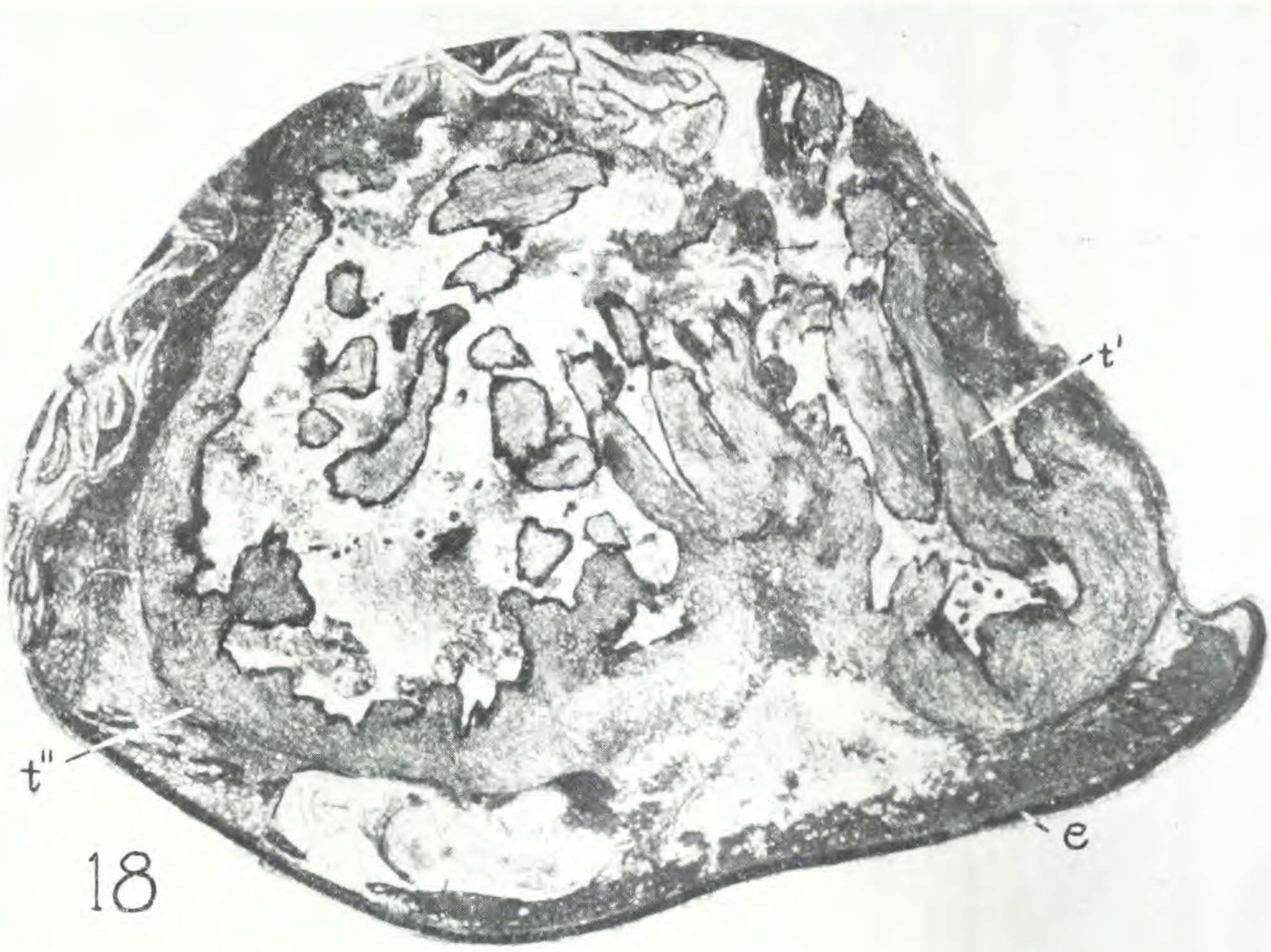
PLATE 39

Nucellangium glabrum

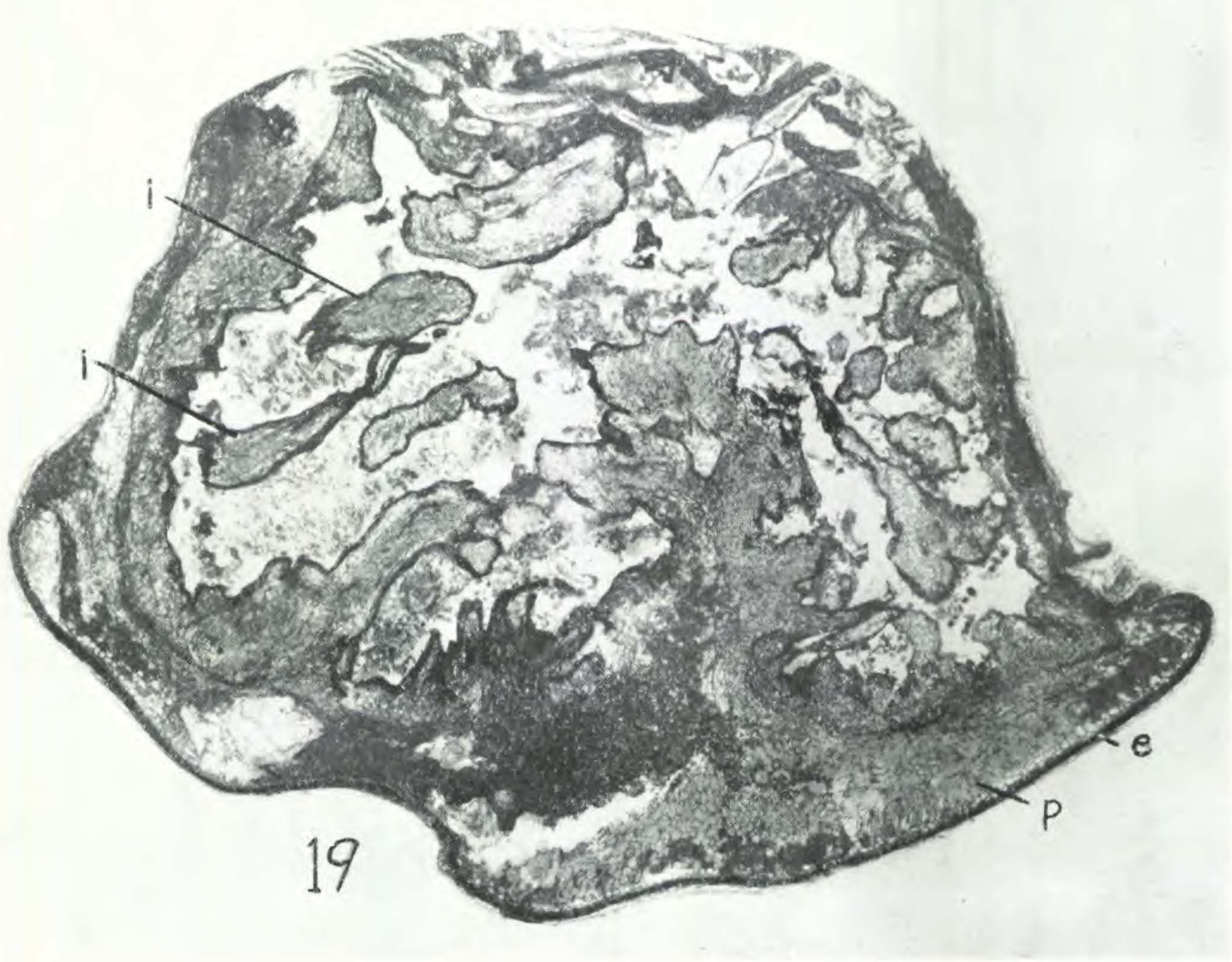
Figs. 18, 19. Photographs of sections of the proliferated specimen described on pages 486–488.

Fig. 18. From peel No. 519.T7 (slide No. 1674): *t'*, vascular strand in proliferated arm (see fig. 14); *t"*, vascular strand in peripheral parenchymatous zone; *e*, epidermis. × 12.

Fig. 19. From peel No. 519.T29 (slide No. 1675): *e*, epidermis; *p*, peripheral parenchymatous zone which is in organic connection with the epidermis (*e*), and from which the proliferated arms arise; *i*, by following through successive peels these scattered "islands" of tissue may be observed to be proliferated from the peripheral parenchyma zone. × 16.



18



19

A REVISION OF THE GENUS HELIOCARPUS L.[1]

KO KO LAY

INTRODUCTION

Heliocarpus has received considerable attention from plant systematists probably because of the perplexing variation found in the genus and because of the few constant characters of taxonomic value. Furthermore, in the herbarium, the specimens are either in fruit or in flower, never both; and when in flower are either hermaphrodite or pistillate. Thus, assigning them to any particular species becomes extremely difficult. Despite a recent taxonomic study of the genus,[2] there is still considerable confusion regarding many species both in the literature and in the herbarium. More than fifty species and varieties have been named thus far, and with the prevalent vagueness in the concept of speciation, there appears superficially to be but two alternatives: either to split the genus into innumerable indistinct and undefinable "species" or to lump them indiscriminately into few categories of scarcely greater reality.

In my study of the genus an attempt has been made to escape this dilemma by clarifying the concept of speciation. However, as this study has been confined entirely to herbarium specimens which represent only very small portions of the woody plants, no definite idea or suggestion as to the individual variations of single plants has been obtained. I have been fortunate enough in being able to study specimens from nearly all the major herbaria both in the United States and in Europe. The standard method of the herbarium taxonomist has been used for the interpretation of the species, and an attempt has been made to identify the fruiting specimens with the flowering ones. As far as possible, no intergrading forms have been considered as worthy of specific rank, and I have tried to group the "species" into fewer categories of perhaps greater biological reality, in the hope that they will be satisfactory both from a taxonomic and from a practical standpoint. The key has been so prepared that it should be usable for both the fruiting and the flowering specimens.

GENERIC RELATIONSHIPS

Heliocarpus L.[3] commonly is referred to the tribe Grewieae[4] of the family Tiliaceae and usually is recognized by its characteristic fruits. The genus is distinct from the other genera of Grewieae except *Triumfetta*. There is no difficulty in distinguishing the two genera when both are in fruit, as the fruits are very dis-

---

[1] An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Arts in the Henry Shaw School of Botany of Washington University.

[2] Watson, E. E. The genus Heliocarpus. Bull. Torrey Bot. Club 50:109. 1923.

[3] Sp. Pl. ed. 1. 448. 1753.

[4] K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. III[6]:29. 1895.